THE DIRECT AND INDIRECT CONTRIBUTION OF SOIL ALGAE TO THE PRIMARY PRODUCTION OF BIOCENOSES

E. A. SHTINA and K. A. NEKRASOVA

Agricultural Institute, Kirov, (U.S.S.R.)

The term « soil algae » (« les algues du sol », « Bodenalgen ») refers to the sum total of various ecological algal groups :

a) terrestrial algae whose abundant growth (as crusts or films) at the soil surface is possible solely under conditions of adequate moisture ;

b) aquatic-terrestrial, which grow at the surface of permanently-damp soil ;

c) soil algae proper found below the soil surface. All the groups of soil-dwelling algae have an important and many-sided effect on soil processes.

To date, the general occurrence of algae as well as their high variety have been established. In fact, in the U. S. S. R. soils over 1 200 algal species have been found, *Cyanophyta* and *Chlorophyta* predominating. *Xanthophyta* and *Bacillariophyta* include fewer number of species (GOLLERBAKH and SHTINA, 1969).

As phototrophic organisms, algae take part in the primary production of ecosystems. At primary stages of soil formation it is algae that settle first on lifeless mineral substrates.

According to the current views, soil algae continue photosynthesis even under conditions of a low light intensity, which ensures their activity below the soil surface among soil particles. Some algal species are capable of optional heterotrophy, turning to the heterotrophic mode of life in dark soil layers. This mode of life, however, causes a much slower growth rate than in the case of phototrophic alimentation, the population density being low.

The direct role of algae in accumulating organic matter is evaluated by population density and biomass indices.

The methods of quantitative estimation of algae have not yet been adequately developed and unified. Two main methods are used (GOLLERBAKH, SHTINA, 1969) :

1. For evaluating the mass of terrestrial crusts and films, algal colonies or filaments are collected from a certain area (commonly 1 cm^2) and weighed. To make an allowance for the admixture of soil particles, the algal organic matter is burned down (RODIN, GOLLERBAKH, 1954).

On determination of the rate of covering, the mass of algae per hectare can be calculated. The drawback of the above-described method lies in the difficulty of extracting algae from the soil as well as the impossibility of estimating the role of certain algal groups.

2. The abundance of algae below the soil surface as well as in films produced by unicell forms is estimated by counting soil suspension cells under the microscope, the suspension having been decanted and centrifuged. Fluorescence microscopy was applied for counting. The algal wet weight (biomass) is calculated, the cells having been counted and the volume determined. Like in hydrobiology, the specific algal weight value is assumed to be 1. Inaccurate as it is, this method appears to be the sole means of representing the algal mass in the soil if only in approximation. *It is evident that the data obtained by these two methods are not only unequal as to their reliability, but they also express different indices. Weighting by the former method yields the evidence for dry matter, whereas by volume calculation after the latter method the data for the algal wet weight are obtained.*

Algal photosynthetic activity on many occasions leads to the accumulation of considerable amounts of organic matter. This role of algae is especially important in those habitats where vegetation is sparse or is absent altogether, large spaces of barren soils being overgrown by algae. Algae have a large share in organic matter production under the following conditions.

1. At initial soil-forming stages on crags, where algae act as primary humus-producers. First, algae are not abundant there, but their organic matter induces the development of other microorganisms, and later that of higher plants.

2. At arid soil surfaces with desert and semi-desert vegetation, ephemeral crusts are formed, mostly of blue-green algae under conditions of short wet periods (table 1).

Takyrs supply a classical example of a habitat where algae are the sole source of organic matter. *A thoroughly-cleaned alga-formed takyr film contains about 500 kg of dry organic matter per hectare* (RODIN, GOLLERBAKH, 1954). According to NOVICHKOVA (GOLLERBAKH *et al.*, 1956) algal organic matter may reach 0.7 t/ha on algal takyrs, and 1-1.4 t/ha on lichen takyrs.

These abundant algal growths on virgin soils are inseparable from the respective phytocenoses (synusia), the specific composition being determined by a certain soil type.

3. Algae act as pioneers in the overgrowth of alluvial soils, forming a continuous thin coating at the surface (table 1). Their activity form likewise the initial succession stage when populating various unkind and eroded soils as well as scorched lands.

The pioneering role of algae is well illustrated by their abundant growths on purely mineral man-made substrates (cf. on building-site dumps, industrial ash-dumps as well as on « Schlamm »).

4. Along with the above-mentioned conditions, large algal populations occur on fertile cultivated soils. Due to the abundant growths of micro-algae, the soil often becoms green in colour in the periods prior to sowing, after taking in the crops, and, sometimes, in the course of plant growth, in between the plants. This « greening » of soil is related to a combination of favourable conditions such as adequate moisture, warmth, the availability of nutrients, and is, consequently, regarded as a forerunner of good crops.

The composition of the algal group causing « greening » is subject to seasonal fluctuations and is also dependent on soil fertilization. Soil « greening » is most extensive in adequately-wet areas (table 2).

TABLE 1

Algal biomass in superficial growths on virgin soils

Soils	Algal groups	Biomass (kg/ha)		Reference
		Wet weight	Dry weight	
Takyrs	*Oscillatoriales*		500	Rodin a. Gollerbakh 1954.
Takyrs	*Oscillatoriales*		1 400	Gollerbakh *et al.*, 1956.
Solonetz crusty	*Cyanophyta*	467		Shtina, 1968.
Solonetz meadow	*Cyanophyta, Diatoma*	515		Shtina, 1968.
Dark chestnut	*Cyanophyta, Diatoma*	511		Shtina, 1968.
Chestnut	*Cyanophyta*	181		Shtina, 1968.
Solonetz soils	*Nostoc commune*	73-217		Bolyshev *et al.*, 1967.
Flood-land	*N. sphaeroides*	800-1 500	60-140	Gollerbakh a. Shtina, 1969.
Flood-land	*Botrydium granulatum*		97.5	Noskova, 1968.
Dern-calcareous	*Nostoc commune*	450-775	142-177	Noskova, 1968.

TABLE 2

Algal abundance in superficial coating on cultivated soils (the rate of covering is taken into account)

Soils	Plants	Dominant algae groups	Cell numbers in thousand per 1 cm²	Biomass in kg/ha	Reference
Dern-podzol	Winter-rye	*Chlorophyta*	up to 19 627	up to 260	Shtina, 1959.
Dern-podzol	Winter-rye	*Chlorophyta* and *Diatoma*	248-1 874		Balezina, 1965.
Dern-podzol	Clover	*Chlorophyta, Cyanophyta*	690-1 934	up to 70	Balezina, 1965.
Dern-podzol	Clover	*Cylindrospermum*	3 109		Shtina, 1968.
Dern-podzol	Oats (stubble)	*Cylindrospermum*	341.3		Shtina, 1968.
		Nostoc	1 259.6		Shtina, 1968.
Peaty-boggy	Spring cereals	*Xanthophyta, Chlorophyta*	700-2 000	up to 750	Kulikova, 1965.
Peaty-boggy	Winter-rye	*Chlorophyta*	up to 7 000	15 000	Kulikova, 1965.
Grey forest soil	Winter-rye	*Cyanophyta*	4 116		Noskova, 1968.

The evidence given in the table appears to have been somewhat underestimated. The calculations were made per hectare of smooth area, the rate of covering index having been taken into account. Actually, algal coating covers the slopes of crests

and furrows ; the algae grow on the surface of large soil clots, occuring in cracks formed when soil gets dry a few cm deep.

Especially abundant algal populations occur on cultivated soils. According to OSMANOVA (1968), superficial films of blue-green algae on cotton-plant fields yield up to 26 g of dry matter per 1 m². Algal biomass in the soils of Indian rice fields was found to range from 0.05 to 0.24 mg per 1 g of the soil (PANDEY, 1965). ARORA (1969) reports that algae produce about 2.24 t of dry matter per hectare on rice-fields.

Algae can also be phototrophic below the soil surface within the light penetration range, even at a very low light intensity. However, their abundance decreases rapidly with depth, the population density becoming meagre at a depth lower than 10 cm. The algal content in the soil is very dynamic, no mean indices being feasible. In fact, for the U. S. S. R. soils it ranges from 3 600 to 1 450 000 cells per 1 g of the soil in the upper layers, the biomass varying from 7 to 500 kg/ha (table 3).

It is evident (table 3) that below the soil surface too the algal wet weight sometimes shows high values. However, all the values cited are solely indicative of one-time biomass, giving no idea of the mean annual algal production.

To calculate the actual productivity of algae during the vegetative period, the growth rate and reproduction rate data must be available, as well as those for the number of generations and organic matter transformation pathways. This evidence is, unfortunately, lacking, although it is known that under favourable conditions algal abundance rapidly increases.

Algal productivity in terrestrial phytocenoses is, naturally, much inferior to

TABLE 3

Population density and biomass of algae in soils

Soils	Phytocenoses	Depth of sampling (cm)	Population density thousand per 1 g of the soil	Biomass (kg/ha)
Humic-iron podzol	Coniferous forest	0-10	5-86	7-20
Dern-podzol	Meadow	0-10	55-208	40-300
Dern-podzol	Crop rotation	0-10	27-258	40-500
Peaty-boggy	Crop rotation	0-10	22-988	20-80
Deep chernozem	Steppe (mown)	0-5	16-47	
Deep chernozem	Tiled soil	0-10	4-141	
Serozem	Cotton-plant field	0-5	37-347	
Zheltozem-podzol	Forest	0-10	30-201	

that of higher plants. However, the importance of algal organic matter lies in its exceptional mobility. The organic matter rapidly accumulated under favourable conditions, is readily involved in diversified soil processes.

The alga-produced organic matter may meet with various fates in the course of further transformations, thus playing different roles in the soil activity.

Evidently, the most essential function of algae is their importance as a diet for heterotrophic microorganisms. Algae constitute the initial links of a number of food chains. It is still in the course of the life-cycle that agal cells attract numerous bacte-

ria. Algal capability of forming jelly colonies as well as of slimy cell membranes and producing slimy sheaths promotes the development of bacteria in these algae. The colonial slime as well as slimy algae sheaths are abundantly populated by bacteria. Various non-sporulating groups are dominant among them, some oligonitrophilous and nitrogen-fixing forms occuring, which suggests the symbiosis of algae and nitrogen fixing bacteria (see the survey by : GOLLERBAKH and SHTINA, 1969). Heterotrophic organisms assimilate carbohydrates as well as other energetic materials contained both in the lime and in lifetime algal excretions.

Therefore, these organisms are permanent algal satellites, populating the cell surface and forming a peculiar « algosphere » around the cells and algal filaments.

The interrelations of algae and bacteria are indisputably more complex and diversified than a common food chain. There is some evidence that algae excrete certain biologically-active agents ; however, this problem has been little investigated.

The inducing effect of algae on the development of bacteria in the soil has been demonstrated by experimental introduction of algae in dern-podzol soil (SHTINA *et al.*, 1967). In all the experiments, irrespective of the subject plant response the introduction of the algae gave rise to an extensive development of a number of bacterial groups.

On many occasions, the algal organic matter proves to be beneficial to the development of microfungi. In fact on takyrs where algae are the permanent and, often, the sole source of organic matter, an exceptional variety of microfungi have been found, which meet there with conditions conducive to a vigorous growth (RODIN, GOLLERBAKH, 1954). As was demonstrated by PARKER and BOLD (1961) the interrelations of algae with fungi depend on nutrition conditions, ranging from the absolute destruction of the alga by the fungus to a long-term symbiosis. The evidence of selective symbiosis of some fungal species with certain species of algae has been obtained. In fact, the alga *Tolypothrix tenuis* has been found to have *Penicillium* species as its satellites ; *Nostoc muscorum* is found together with *Fusarium* species (BAZHINA, SHTINA, 1967).

To date, little has been known of animal algophagi. It has been noted (BIRCH, CLARK, 1953) that algae are consumed by a considerably smaller part of the microfauna as compared with bacteria, i. e. — Protozoa and Nematoda. However, the cultivation of abundant algal growths is often hazarded by alga-feeding microfauna forms (VENKATARAMAN, 1961).

In our experiments, the microscopy of soil alga accumulative cultures revealed a repeated extensive destruction of algae by amoebae, infusoriae and nematodes.

When growing algae on membrane nitrocellulose filters (NEKRASOVA, 1969) populations of Protozoa and Acarina have been repeatedly found on the growths of various algal forms. In some experiments it took the *Protozoa* and *Acarina* under investigation 5-7 days to produce abundant populations which lead to the perfect elimination of algae at the filter surface. Observations on amoebae diet preferences with respect to different algal groups have revealed that the green algae — *Chlorella terricola, Scenedesmus quadricauda* and *Hormidium flaccidum* are most extensively consumed by amoebae ; a decrease in algal abundance on the filters or their perfect elimination could be recorded from visual observations. Microscopy revealed that amoebae were filled with the cells of these algae (fig. 1). Other algal species (*Nostoc muscorum* and *Characiopsis* sp.) were consumed by amoebae much less actively.

Instead of « swallowing » the cells of these algae, the amoeba could be seen clinging to them (fig. 2). Evidently, having dissolved these algae, the amoeba were feeding on them.

FIG. 1. — Amoeba *filled with the cells of* Hormidium flaccidum

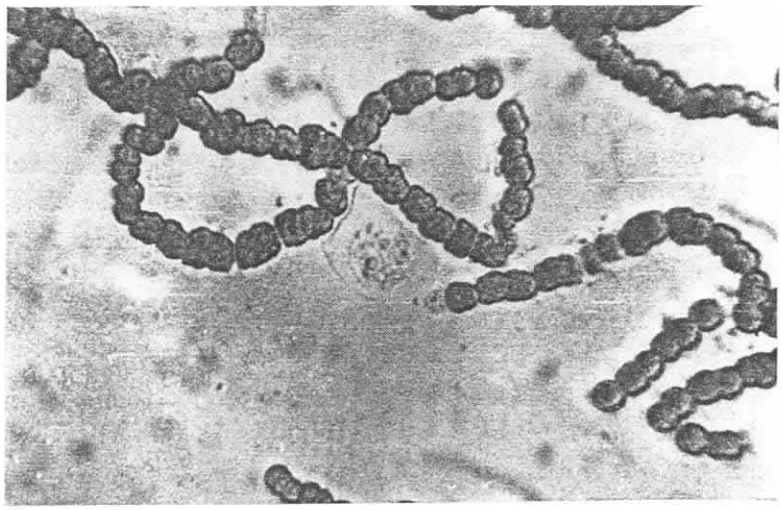

FIG. 2. — *Filaments of the alga* Nostoc muscorum *with an* amoeba *clinging to them*

The most extensive feeding of amoebae on algae was recorded on two occasions as follows :

1. on weakened algal cultures and ;

2. the soil moisture exceeding 70 p. 100 of the maximum water-holding capacity. Peculiar protozoan forms were found on Cyanophyta which we failed to identify. These animals were found to be responsible for a rapid lysis of the vegetative algal cells without affecting the heterocysts. It is noteworthy that amoebae do not affect the heterocysts either.

Large mite populations of the genus *Tyrophagus* (*Tyroglyphidae*), were revealed on the aggregations of some algal species. These mites formed specific « pastures » with large amounts of eggs. Similar mite « pastures » although formed by fungi and bacteria have been reported by ARISTOVSKAYA (1965). Mites populated all the algal

species under investigation. Abundant reproduction, however, was recorded for the cultures of the species *Chlorella terricola, Scenedesmus quadricauda* and *Characiopsis* sp. This observation gives ground to believe that numerous animal algophagi exist under natural conditions as well.

Thus, soil algae stimulate microflora and microfauna, acting as main organic matter producers, in a number of soil microbiocenoses.

The activity of various microorganisms being related to algae, the latter have an indirect effect on the productivity of the biocenosis, since they affect plant life conditions.

Nitrogen accumulation which is beneficial to the growth of higher plants is also illustrative of the algal indirect contribution to the primary production of the biocenosis. Soil algae are important in nitrogen accumulation both indirectly — through the stimulation of nitrogen-fixing bacteria, as has been outlined above, and directly — through elementary nitrogen fixation.

As nitrogen-fixing microorganisms, algae are of particular interest since the algal cell combines the ability of photosynthesis and that of assimilating molecular nitrogen. In contrast to heterotrophic nitrogen-fixing organisms, algae do not depend on ready organic matter.

It is only certain *Cyanophyta* species that can fix nitrogen, those which have heterocysts. To date, experimental evidence has been obtained on nitrogen fixation in 82 species. Most of them, in particular *Nostoc, Anabaena, Cylindrospermum* are wide-spread and frequently abundant on crags, in soils (table 1 and 2) and in rice fields. Soil cultivation invariably gives rise to an extensive development of nitrogen-fixing algae.

The estimation of the nitrogen accumulation rate under field conditions presents much difficulty. Therefore, only very rough values have been obtained for the rate of algal nitrogen fixation. It should be noted that under natural conditions the nitrogen-fixing activity of *Cyanophyta* can hardly be delimited from that of their satellites — nitrogen-fixing and oligonitrophilous bacteria. On the other hand, algal nitrogen fixation is sometimes stimulated by bacteria which cannot assimilate elementary nitrogen (Bunt, 1961). Thus, nitrogen accumulation is dependent on the activity of the whole nitrogen-fixing complex with *Cyanophyta* at the basis.

Most of the evidence obtained on nitrogen accumulation refers to rice fields. There algae fix up to 90 kg of nitrogen per hectare annually (Singh, 1961).

In our experiments N^{15} fixation by algal crusts collected from different soils of the U. S. S. R. was tested. The accumulation of the labelled nitrogen was found only in those samples where nitrogen-fixing algae *Nostoc, Anabaena, Tolypothrix* predominated.

The effect of nitrogen-fixing algae on the growth of higher plants has been repeatedly tested in field and vegetative experiments (Singh, 1961 ; Watanabe, 1965 ; Shtina *et al.*, 1967 and others). The introduction of algae into the soil has on most occasions lead to a better plant growth as well as increase in crops (rice, sugarcane, barley, rye, oats, peas have been tested). It is suggested that the effect of algae on the crops is not confined to the nitrogen-fixing activity only, but it is also related to the excretion by algae of growth-stimulating agents.

RÉSUMÉ

CONTRIBUTION DIRECTE ET INDIRECTE DES ALGUES DU SOL A LA PRODUCTION PRIMAIRE DES BIOCÉNOSES

Les algues du sol contribuent à la production primaire des biocénoses à la fois directement et indirectement. Par leur activité de photosynthèse, les algues produisent une grande quantité de matière organique, aussi bien dans les couches supérieures du sol qu'à sa surface ; cette production n'a pas encore été estimée. La matière organique des algues est à la base de certaines microbiocénoses, lesquelles déterminent les effets indirects des algues sur la productivité de la biocénose.

La fixation d'azote, réalisée par certaines algues Cyanophytes est également importante du point de vue de la productivité de la phytocénose. Expérimentalement, on a obtenu une amélioration de la croissance, ainsi que des augmentation de récoltes, grâce à l'activité d'algues fixatrices d'azote.

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DISCUSSION

G. JAGNOW : Have you been able to show, that soil algae can grow in the dark in soil in the presence and under the competition of the natural mixed bacterial flora ?

E. A. SHTINA : Some species of soil algae may be facultatively heterotrophous and exist in the darkness. As it has been shown by Parker (1961), in such conditions algae are associated with heterotrophous bacteria.

P. LEBRUN : Il semble, d'après vos mesures de biomasses, que les algues forment une source alimentaire très grande et constituent un important point de départ de diverses chaînes trophiques. Est-ce que vous pouvez me donner un ordre de grandeur de l'utilisation de cette source de nourriture par les Acariens Oribates ?

E. A. SHTINA : Nous n'avons pas de données sur la quantité d'algues consommée par les Acariens.